DESCRIPTION AND CONSERVATION STATUS OF A NEW SUBSPECIES OF CICINDELA TRANQUEBARICA (COLEOPTERA: CICINDELIDAE), FROM THE SAN JOAQUIN VALLEY OF CALIFORNIA, U.S.A.¹

C. Barry Knisley² and R. Dennis Haines³

ABSTRACT: This paper describes a new subspecies of oblique-lined tiger beetle, Cicindela tranquebarica joaquinensis, from the San Joaquin Valley of California. This new subspecies is most closely related to C. t. vibex with which it intergrades along the margins of the San Joaquin Valley. The maculation pattern of C. t. joaquinensis, like that of C. t. arida is characterized by being reduced to only the apical lunules. However, C. t. arida is significantly smaller in body size, has microserrations on the elytra, is restricted to the Death Valley area and thus well separated from C. t. joaquinensis by both distance and the Sierra Nevada Mountains. A study of collection records indicated C. t. joaquinensis was historically present throughout much of the San Joaquin Valley in alkali sink or flat habitats. A search of the historic and many additional sites with these habitats produced only three extant populations of C. t. joaquinensis, all in patches of habitat that were less than three hectares in size. The extirpation of most populations of this beetle was caused by habitat loss from intense agricultural development in the San Joaquin Valley, especially cultivation for crops, cattle grazing, and water diversions and modifications related to irrigation. Increased vegetation is also reducing the open areas in the habitats needed by this species. Because of the very few and small extant populations and the elimination of nearly all of the alkali sink habitat, C. t. joaquinensis should be considered for endangered status by the U.S. Fish and Wildlife Service.

KEY WORDS: tiger beetle, *Cicindela tranquebarica*, Cicindelidae, Coleoptera, insect conservation, rare insects, San Joaquin Valley, California, U.S.A.

Tiger beetles (family Cicindelidae) have become increasingly important as a focus group in insect conservation, particularly as indicators of biodiversity and habitat degradation (Knisley and Hill 1992, Pearson and Cassola 1992, Pearson et al., 2006). At present, four species of tiger beetles are listed as endangered or threatened and two others are candidates for listing. An additional 25 or more species and subspecies of tiger beetles may be sufficiently rare to be included on the list of threatened or endangered species (Knisley and Schultz 1997, Pearson et al. 2006). Although both species and subspecies may be listed under the Endangered Species Act, determining the taxonomic status is necessary because it affects listing priority and action. For example, taxonomic studies were a critical part of the status surveys and listing considerations for all of the currently listed or candidate tiger beetles (*C. dorsalis dorsalis, C. puritana, C. ohlone, C. albissima, C. nevadica lincolniana,* and *C. highlandensis*).

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The oblique-lined tiger beetle, Cicindela tranquebarica, is one of the most widespread and diverse of the U.S. tiger beetles. Over 27 names have been applied to it, and the 12 subspecies recognized by most workers are more than any other North American species. Eleven of the subspecies occur west of the Great Plains, including 10 in the southwest, and 6 of these in California (Pearson et al., 2006). The most distinctive character of this species is the extended anterior maculation (humeral lunule), which is long and angles gradually inward from the outer edge of the elytron, and the absence of a marginal white line (Pearson et al., 2006). However, several populations have the maculations reduced to only a small apical lunule at the posterior tip of the elytra. Dorsal coloration varies from black, brown, red, and green to bluish-green. Of the five subspecies that are restricted to or range into southern California, C. t. vibex is the most widely distributed. It ranges from British Columbia south through California and west of the Sierra Nevada to San Luis Obispo and Ventura Counties. Most of the specimens in collections from the San Joaquin Valley have been identified as C. t. vibex. C. t. sierra is a widespread montane form (occurring above 200 m) and ranging from far eastern Tulare County north to Lassen County in northern California. C. t. inyo is restricted to the Owens Valley of eastern California and adjacent Nevada, while C. t. viridissima is in Orange, Los Angeles, Riverside, and San Bernardino Counties.

The most recent taxonomic study of C. tranquebarica by Kritsky and Horner (1998) recognized eight subspecies and elevated C. t. arida to full species status. These workers considered C. t. moapana and C. t. inyo to be synonyms of C. t. parallelonota, and C. t. borealis a synonym of C. t. vibex. Most cicindelid workers, especially those familiar with the diversity of forms in southern California, including some populations not examined by Kritsky and Horner (1998), believe their study was not thorough enough to justify the taxonomic revisions they present, and that much additional work on this species is needed, possibly including mtDNA or other new approaches. Consequently, we follow the most widely accepted treatment of this species as given in Boyd et al. (1982), Freitag (1998) and Pearson et al. (2006). Adding to the problem is that many California populations have apparently been extirpated in the past several decades, most likely due to the widespread conversion of natural habitats to agricultural or urban uses. Regardless of whether or not the revisions of Kritsky and Horner (1998) become widely accepted, the new subspecies we describe was apparently unknown by those authors and a distinct subspecies of C. tranquebarica. Our study was prompted by the extreme rarity of this new form and the need to protect it from extirpation.

METHODS

The initial part of this study included a compilation of information on the distribution of the southern California populations of *C. tranquebarica* by reviewing the literature and examining collection records and specimens from various museum, university, and private collections that had specimens of this species from southern California. Specimens we examined were from the following collections:AMNH – American Museum of Natural History, New York, NY; CASC – California Academy of Sciences, San Francisco, CA; CBKC – C. Barry Knisley Collection, Ashland, Virginia; CSCA – California State Collection of Arthropods, Sacramento, CA; DBC – David Brzoska Collection, Naples, Florida; LACM – Los Angeles County Museum, Los Angeles, CA, California; RDHC – R. Dennis Haines Collection, Tulare, California; TCAC – Tulare County Agricultural Commissioner/Sealer's Office, Tulare, CA; UCRC – University of California, Riverside, Riverside, CA; UID – University of Idaho, Moscow, ID.

Taxonomic Studies: Our taxonomic study was based primarily on population differences in maculation pattern and color because these are the characters most commonly used by other workers to distinguish subspecies of *C. tranquebarica*. To evaluate differences in maculation pattern among populations we graded specimens (usually 10-20 per population, if available) according to the range of maculation patterns of *C. tranquebarica*, from the most fully maculated (Fig. 1A) to the least maculated (Fig. 1H). Other variations of the maculation pattern included in the analysis were width at the base of the middle band, connection of the humeral dot with the humeral lunule, and connection of the apical dot with the apical lunule (Fig. 1). Dorsal ground coloration was also a variable character and included in the analysis. Mean total body length differences were not statistically significant for all populations examined except for *C. t. arida*, which was significantly smaller than all other populations. Setal patterns and several other characters of potential importance were examined but were similar in all populations and thus not useful for separating populations.

Field Surveys: The diversity of habitat types utilized by C. tranquebarica presented a challenge for obtaining an accurate determination of its preferred habitat and distribution within our survey area. Some of the historic label data was too general to identify specific localities and habitat type, but fortunately one of us (RDH) obtained firsthand information from several of the early collectors about their collecting sites in the San Joaquin Valley. With this information and visits to many C. tranquebarica sites in southern California, we concluded this species occurred almost exclusively in two types of habitats, both having moisture at or near the surface. Most records were from sandy floodplains along rivers or streams, but others were from alkali sinks, flats, and playas, so we concentrated our field surveys on these two habitat types. We conducted fieldwork on >30 dates from summer of 2002 through spring 2006, primarily from March through May and September through November. This is the bimodal period of adult C. tranquebarica activity indicated by collection records. In our visits to these sites, we searched the open areas of potential habitat for adults, made spot checks of the ground surface for larval burrows (Knisley and Schultz 1997) and recorded habitat features that were probable indicators of habitat for C. tranquebarica. Most sites with potential habitat were visited 2-4 times. At the sites where we found C. tranquebarica, we recorded dominant plant species and other habitat characteristics and conducted visual searches and counted the numbers of adults and larvae present. Representative specimens were collected for the description, but because of its rarity, only limited numbers were taken and most of these later in the year after they had time to mate and oviposit.

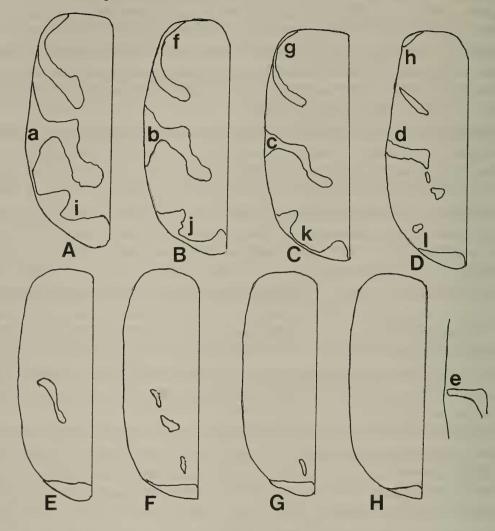


Figure 1. Illustrations of the variations of maculation patterns for *C. tranquebarica* throughout its range. Capital letters indicate middle band and overall maculation pattern, arranged from most (A) to least developed maculations (H). Small letters (a to e) indicate variations in the width at the base of the middle band; f, g, h are variations in attachment of humeral lunule; i, j, k, l are variations in apical lunule. See Table 1 and text.

RESULTS AND DISCUSSION

Cicindela tranquebarica joaquinensis Knisley and Haines, new subspecies

(Fig. 2)

Description: Holotype male. Length 12.8 mm, robust. Color green dorsally; ventrally head and thorax shiny metallic green, abdomen metallic blue; vertex, frons and clypeus shiny, metallic green. Elytral maculation reduced to only a small apical lunule. HEAD: Labrum ivory with black margin, three labral teeth of equal

size, with 6-7 marginal setae. Mandibles with basal and apical portion black, middle portion green, with 3 teeth. Frons rugose with abundant (>50) erect setae; vertex rugose, and with dense, erect setae; gena rugose especially near eye, with 1-2 indistinct setae on anterio-ventral margin. Antennal segments one to four metallic green; segment one with 19-25 setae, segment two with 1 apical setae; segments three and four each with rows of long setae along the lateral margin and apex; segments 5-11 are testaceous and dull brown. THORAX: Pronotum rectangular, widest anteriorly; disc covered with shallow wavy rugae; median line shallow, anterior and posterior transverse grooves deep; long, thin, erect setae along marginal third of disc. Prosternum glabrous; proepisternum with abundant long, thin setae; mesepisternum and mesepimeron with many long, erect setae. Metasternum and metepisternum with long, erect setae. ELYTRA parallel sided, surface finely granulate, covered with raised gold bumps; deep setae bearing fovea. Apices without microserrations, but with a short spine. ABDOMEN: Terminal three sternites shiny metallic green with scattered long erect setae, most along posterior margin. LEGS: Pro- and mesocoxa with long, erect setae; metacoxa with long, erect setae along dorsal anterior margin; pro- and mesotrochanter with long, erect setae on posterior margin; metatrochanter glabrous.

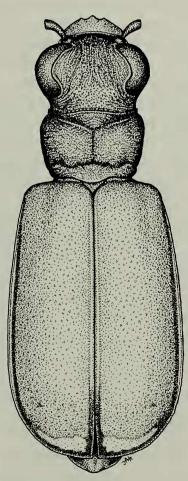


Figure 2. Habitus of male holotype of *Cicindela tranquebarica joaquinensis* Knisley and Haines.

Type Material: Holotype (male), CA, Kings Co., near Guernsey, 27-III-2005. Paratypes: 10 from CA, Tulare Co., west of Earlimart, 17-XI-2005; 12 from CA, Kings Co., near Guernsey, 27-III-2005. Holotype and 5 paratypes to be deposited in California Academy of Sciences; 6 paratypes to USNM, 3 to AMNH, 8 to the authors (4 each to RDH and CBK).

Variation of type series: Males: Mean length, 11.8 mm, range of 11.1 to 12.2 mm. Females: Mean length, 12.6 mm, range of 11.8 to 13.2 mm. A small percent of specimens have a dot-like or faintly developed partial middle band or a detached part of the apical lunule. Setae on first antennal segment range from 12 to 28, most individuals with 18-24. Number of setae on anterio-ventral edge of gena ranges from 0-4. Sixth abdominal sternite in females lacking fine pubescence and long, erect satae.

Comparison with other populations. Although the maculation pattern of C. t. joaquinensis is most similar to that of Cicindela t. arida (Table 1), our study indicates this new subspecies is most closely related taxonomically to C. t. vibex but differs in maculation (see below). Despite the nearly identical maculation patterns of C. t. joaquinensis and C. t. arida and green coloration, most of the C. t. arida we examined also had a reddish cast or sheen over the green. More importantly, Cicindela t. arida has microserrations on the elytral apices and is significantly smaller (p < 0.001, ANOVA) than C. t. joaqinensis in both elytral length (mean of 7.34 mm, s.d.= 0.19, versus 8.37 mm, s.d. = 0.44, in females and 6.58 mm, s.d.= 0.35 versus 7.65 mm, s.d.= 0.27, in males) and elytral width (4.69 mm, s.d = 0.26versus 5.29 mm, s.d. = 0.29, in females and 4.28 mm, s.d. = 0.28 versus 4.88 mm, s.d. = 0.18, in males). Populations of all other western subspecies that we measured were not significantly different in elytral length or width from C. t. joaquinensis. Previous studies of tiger beetle subspecies have established a precedent for body size as an appropriate taxonomic character. For instance, body size was used to separate the subspecies of C. dorsalis (Boyd and Rust 1984). These differences may also function as a reproductive isolating mechanism. In laboratory mating studies of C. d. dorsalis and C. d. media, the size difference between these two subspecies reduced pairing success and mating times (Fielding and Knisley, unpublished studies). That study also found that the size mismatch of the flagellum of the male aedeagus and the spermathecal duct of the female (into which the flagellum inserts during sperm transfer) might reduce the chances for successful sperm transfer in intersubspecific matings. The size difference between C. t. arida and other western subspecies is comparable to that of C. d. dorsalis and C. d. media, and may similarly function as a reproductive isolating mechanism. The structures of the male genitalic components of C. t. arida were similar to other C. tranquebarica but their smaller size and was a key factor in the separate species status (Kritsky, pers. comm.). Further evidence that C. t. joaquinensis is less related to C. t. arida than to C. t. vibex is the great distance (over 220 km) and the presence of the Sierra Nevada Mountains that would act as a significant barrier to gene exchange between populations in the San Joaquin Valley and Death Valley. The similarity of the elytral maculation pattern in these two subspecies may thus be a result of convergent

evolution rather than taxonomic similarity. Also, the differently colored and maculated subspecies of *C. t. inyo* from the Owens Valley occurs west of Death Valley and between the ranges of *C. t. arida* and *C. t. joaquinensis*.

Of the 88 specimens from the seven populations within the San Joaquin Valley examined, 59 had only apical maculations (Fig. 1, grades G or I) and 15 others had, in addition, a very reduced or incomplete middle band, usually represented by one or two dots or short lines (grades D, E, F). Only 14 specimens had a complete middle band (grades B, C) with a wider base (grades c, d). Most of these were from Coalinga at the western edge of the San Joaquin Valley or from the Dinuba-Reedley populations at the eastern edges of the San Joaquin Valley, and probably intergrades of C. t. vibex and C. t. joaquinensis. A range of maculation patterns was present among specimens from Kern County, but most of these had a well developed middle band (B) and humeral maculations (f, g) and were similar to populations further south (Soda Lake in San Luis Obispo County) or to the east (Lake Isabella in eastern Kern County) (Table 1). Most workers have identified these populations as C. t. vibex, but additional studies are needed, probably using mtDNA analysis, to confirm this and to determine their relationship to other southern California populations. In addition to C. t. viridissima and C. t. sierra, there are brown, well maculated populations from the Cuyama Valley of western Ventura County, similar brown populations along the Mojave River in western San Bernardino County, and well-maculated green to blue green populations along the Santa Clara River in eastern Ventura County. The identity of these forms is uncertain, and they apparently were not included in Kritsky and Horner's (1998) study of C. tranquebarica. One additional character that distinguishes C. t. joaquinensis from all other C. tranquebarica subspecies we examined, including those in Table 1, is the lack of microserrations on the elytral apices.

Historic and recent records: Our examination of San Joaquin Valley C. tranquebarica specimens in collections produced a total of 46 site records within the range of C. t. joaquinensis, including 3 records for Madera County, 19 for Tulare County, 2 for Kings County, 21 for Fresno County, and 1 from Stanislaus (Table 2, Fig. 3). Most of these records were from the 1920s to 1940 (many collected by F. T. Scott and R. Hopping). The most common collection sites were Coalinga (8 records), Visalia (7 records), and Kerman (6 records). Coalinga is along the western edge of the San Joaquin Valley. Specimens from there are more maculated, and probably intergrade with C. t. vibex (see above). The most recent records for C. t. joaquinensis were from March 1984 and April 2000. The 2000 record was for a small population found in scattered patches of alkali sink habitat in southern Madera County (Christopher Rogers, pers. comm.). The 1984 record was for several specimens found along a sandy road through an alkali meadow in the Kaweah Oaks Preserve, near Farmersville (Tulare County), by the second author. The only other recent records for C. tranquebarica within the San Joaquin Valley are two specimens taken along the Kings River near Reedley (October 2003) and one from Dinuba (1988). All three of these specimens have more complete maculations suggesting they are intergrades with C. t. vibex.

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n	uncertain	7	5							9	9				
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County	Locality	No.	Date	Collector	Collection
Madera	Chowchilla	1	7-111-39	R. P. Allen	AMNH
Madera	Granite Cr.	1	6-V-34	C D	AMNH
Madera	20 km W of Borden	6	10-IV-2000	C. Rogers	DBC
Fresno	Fresno	1	20 111 1004	E. A. Schwartz	USNM
Fresno	Farmerville		30-III-1984	D. Haines	RDHC
Fresno	Kerman		19-III-1933		TCAC
Fresno	Kerman		30-X-1927		TCAC
Fresno	Kerman		15-X-1927		TCAC
Fresno	Kerman		15-X-1927		TCAC
Fresno	Kerman	1	30-X-27	M. A. Cazier	AMNH
Fresno	Kerman	_	19-III-1933		TCAC
Fresno	9 mi W. Kerman	1	25-III-53	Snelling	CDFA
Fresno	Helm		16-III-1924		TCAC
Fresno	20 mi. SW Fresno	1	4-11I-38		LACM
Fresno	Parlier, Kearney Agr. Center, Fresno	5	9-X-89	N. J. Smith	CDFA
Fresno	Coalinga		V-5		TCAC
Fresno	Coalinga		15-III-1927		TCAC
Fresno	Coalinga				TCAC
Fresno	Coalinga		V-5		TCAC
Fresno	Coalinga		20-111-62		CALAC
Fresno	Coalinga	2	27-X - 83		N Smith
Fresno	Coalinga	3	30-111-40		NLRC
Fresno	Coalingua, Los Gatos Ck.	4	7-IV-73		UCR
Fresno	Parkfield Grade, 10 mi SW Coalingua	2	27-X-83		CDFA
Tulare	San Joaquin Mill	1	5-IV-05		AMNH
Tulare	San Joaquin Mill	2	5-V-10		AMNH
Tulare	San Joaquin Mill	1		H F Wickham	LACM
Tulare	San Joaquin Mill	3		Hopping	UCR
Tulare	Kaweah Oaks Preserve	3	1-84	D. Haines	RDHC
Tulare	Visalia			F. Scott	TCAC
Tulare	Visalia		IV-34	F. Scott	TCAC
Tulare	Visalia		IV/1926?	F. Scott	TCAC
Tulare	Visalia		IV-34		TCAC
Tulare	Visalia		IV-30	F. Scott	TCAC
Tulare	Visalia	2	V-34	F. T. Scott	LACM
Tulare	Visalia	2	33?	F. T. Scott	CDFA
Tulare	Exeter	1	28-111-34	A. Nicolay Colln.	USNM
Tulare		1	V-30	F. T. Scott	LACM
Tulare	Exeter	5	28-11-34	M. A. Cazier	AMNH
Tulare		2	111-30	F.Scott	TCAC
Tulare	Exeter	1	3/21/1934?		TCAC
Tulare	Skaggs Bridge	1	10/13/1929		TCAC
Tulare	Porterville	2	1/V/1957	WM.R.Clark	TCAC
Kings?	"North Kamm"	3	25-111-32	A. T. McClay	USNM
Kings	2 mi S. Hub		7-VI-78	?	
Kern	Cottonwood Cr.	2	6-IV-39	W. F. Barr	USNM
Kern	?	1		H. Morrison	USNM
Kern	Cottonwood Cr.	2	22-III-40	W. F. Barr	LACM
Kern	Cottonwood Cr.	1	6-1V-39	W. F. Barr	LACM
Kern	Cottonwood Cr.	5	22-111-40	W. F. Barr	NLRC
Kern	Cottonwood Cr.	1	6-IV-39	L. L. Jensen	MCZ
Kern	Bakersfield	4	27-11-1892	F. C. Bowditch	LACM
Kern	Poso Cr., 3 mi. E. Hwy 65	14	17-IV-71		LACM
Kern	Poso Cr., 3 mi. E. Hwy 65	12	10-V-71	C. E. Langston	LACM
Kern	Poso Cr., 3 mi. E. Hwy 65	40	17-IV,22-III	U	UCR
Kern	Poso Cr., Snyders Swamp	2	29-III-70	Rumpp	NLRC
Kern	Poso Cr., Snyders Swamp	1	19-IV-75	Rumpp	NLRC
Kern	Kern R.	1	15-IV-05	Hopping	LACM
Kern	Kern R.	1	16-IV-05	Hopping	LACM
Kern	Kern R.	1	1V-28	11 0	LACM
Kern	Oil City	3	1V-16		LACM
Kern	Oil City	1	IV-28	R. Hopping	LACM
Kern	Adobe Station		19-IV-05		UCR
Kern	Kern R.	1	IV-28		LACM
Kern	Cuyama Rch, Cuyama Cyn.	26	6-111-37	M. Cazier	AMNH
Kern	Bakersfield	4	12-III-34		AMNH
Kern	4mi W Bakersfield	10	28-X-75		UCR
	s Turlock	6	?		UCR

Table. 2. Collection records for C. tranquebarica within the San Joaquin Vall	ey.
Locations of current C. t. joaquinensis populations are not included.	



Figure. 3. Map of southern California showing sites for *C. tranquebarica* populations and named subspecies. Letters indicate *C. t. joaquinensis* sites: C = Coalinga, D = Dinuba, E = Earlimart, F = Farmersville, G = Guernsey, H = Helm, K = Kerman, M = Madera, P = Portersville, V= Visalia. Open circles indicate probable intergrade populations of*C. t. joaquinensis*x*C. t. vibex*; solid circle is Cuyama River population; solid triangles are Santa Clara River populations; open squares are*C. t. viridissima*; open triangles are Mojave River populations; solid inverted triangle is*C. t. inyo*; solid squares are*C. t. arida*.

Field surveys and habitats: Using these historical site records, we focused our initial search of extant populations on historic riparian and alkali sink sites within the four-county area, and on additional sites in adjacent counties where these habitats were represented. Over 80 sites were visited (Table 3). Those located along rivers and creeks were the most common among the records and

	Site Characteristics, Comments	heavy use, wide sandy edge, N. side deposits, resurvey	channelized, sandy levee, vegetated, no water		native undisturbed	roads and opens areas, S side of road	3 other sites east of Mendota WMA	Channelized sandy levee, vegetated, no water	heavy use, wide sandy edge, N. side deposits, resurvey	Extensive sandy, dry, heavy use, ORVs	sandy, dry riverbed	extensive sandy, dry, heavy use, recheck		series of historic habitat patches, now all agriculture	historic site, no habitat seen	disced and planted to grain	disced and planted to grain	heavy disturbance from cattle, had flowing water in 1983		needs further survey	disced and planted to grain	disced and planted to grain	disced and planted to grain	disced and planted to grain		dry creek bed	channelized	channelized		channelized		C. haemorhagica	C. haemorhagica					heavy grading, ORV activity, sandy
ouquinensis.	Habitat	alkali sink	creek edge	alkali sink	alkali sink	alkali sink	alkali sink/grassland	Floodplain	Floodplain	Riverbed	Riverbed	Riverbed	Riverbed	alkali playa	alkali playa	alkali playa	alkali playa	dry sandy wash		sandy wash	alkali playa	alkali playa	alkali playa	alkali playa	large sandy wash	sandy wash	sandy wash	sandy wash	sandy wash	stream	streambed/saltgrass	streambed/saltgrass	streambed/saltgrass			river edge	river edge	river edge
es suiveyen ioi c. 1. jouquinensis	Date	10/04, 3/26/05	2/11/2004	3/13/04, 4/2/05	3/13/04, 4/2/05	3/13/04, 3/27, 4/2/05	3/13/2004	2/13/2004	2/11,3/14/04,3/26/05	2/12/04, 3/13/2004	2/12/04, 3/13/2004	3/14/2004	3/14/2004	4/2/2005	3/13/2004	4/2/2005	4/2/2005	4/25/2004	4/25/2004	2/12/2005	4/2/2005	4/2/2005	4/2/2005	4/2/2005	3/26/2005	3/26/2005	4/1/2005	3/26/2005	4/25/2004	4/25/2004	5/29/2005	5/29/2005	5/29/2005	3/30/2005	3/30/2005	3/31/2005	3/31/2005	3/28/2005
ladie 3. Locations and nadital notes for all sites	Site Location	Avenue 12, S. side, near Rd. 19	Hwy 145 x Cottonwood Ck.	Rt. 180, 6 mi W. Rt. 145, N side	Rt. 180, 9 mi W. Rt. 145, S side	Mendota Wildlife Area, public access, off 180	Jameson, James Rd & Hwy 180	Rt. 145 x Cottonwood Ck.	Rt. 145 x San Joaquin River, Skaggs Bridge	E of Hub, Kings R. x Excelsior Ave.	E of Hub, Kings R. x Maple St.	Laton x Kings R.	Kingsburg, Rt. 201 x Kings R., Elmonte Way (J-40)	SW Kerman, N and S of American Ave.	Helm	Helm, E of 145, N of Kamm	Helm, North of Kamm, section 17	Coalinga, SE of, Parkfield Grade	Coalinga,SE of, Rt. 198, Wartham Creek	Coalinga, S of, Jacillitos Creek at Lost Hills Rd.	Coalinga, NE of, Los Gatos Ck near Salt Canyon	Coalinga, NE of, Los Gatos Ck near Gale Ave	Coalinga, N of, Palmer Ave.	Coalinga, E of, Calaveras Ave.	E of Coalinga, Arroyo Pasajero, Phelps Ave.	Coalinga, E of, Jayne Ave x Chino Ck	Coalinga, E. of, Los Gatos Ck. at Phelps	Coalinga, Warthan Crk & Jayne Ave	Coalinga, Oil City, Los Gatos Creek	Coalinga, Los Gatos Creek Park	Little Panoche Valley, L. Panoche Ck at J-1	Little Panoche Valley, L. Panoche Wildlife Area	Little Panoche Valley, S. Fork L. Pan Ck. at J-1	SW Lemoore, E side Hwy 41, N and S of Jackson	SW Lemoore, Murphy Ranch Rd., S of Hwy 198	Clarks Fork (S) Kings River at Rt. 41	North Fork Kings River at Rt. 41	Kings K. x Maple St., W of Laton
ן מטוכ	County	Madera	Madera	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Fresno	Kings	Kings	Kings	Kings	Kings

Table 3. Locations and habitat notes for all sites surveyed for C t ioaguinensis.

river bank to bank, no habitat river bank to bank, no habitat soft saline lake edge Salicornia soft saline with Salicornia too wet too wet disced disced old dairy site off-road course eucalyptus grove Sandy road near Kaweah River and riverbed same habitat, nothing adult seen along sandy edge heavy cattle use	heavy cattle use disced, but not planted overgrown with invasive species, future landfill, resurvey overgrown with invasive species, future landfill, resurvey overgrown with invasive species, future landfill, resurvey well maculated adult burrows, summer cattle grazing winter cattle use disced, but not planted disced, but not planted disced, but not planted winter cattle use summer cattle use summer cattle use disced, but not planted disced, but not planted disced, upland areas grazed dry creekbed, coarse sand, little edge diry creekbed, coarse sand, little edge
river edge river edge river edge vernal pool alkali sink alkali sink alkali sink sandy road, floodplain saltgrass mdw saltgrass mdw	sandy streambed alkali playas saltgrass mdw alkali grassland alkali grassland parking lot alkali playas alkali playas alkali playas alkali playas alkali playas alkali playas alkali playas alkali playas alkali playas alkali sink sandy floodplain sandy floodplain alkali sink
3/28/2005 3/28/2005 3/28/2005 3/28/2005 3/29/2005 6/1/2005 6/1/2005 6/1/2005 6/1/2005 2004, 2005 1an-84 3/13/2004 3/13/2004 3/13/2005 05/2005	Mar-06 4/26/2005 3/05 4/29/2005 4/29/2005 3/14/04 3/14/04 3/14/04 3/14/05 4/30/2005 4/24/2005
Kings R. at Laton, Kingston Regional Park Kings R. x Rd. to Stratford, Rt. 41 Kings R., w side of Rt. 41 Kings, E side, Rt. 41 W of 137, west end of Avenue 224 E side of Corcoran Irrig. District Reservoir S end Rd. 32 along Lakeland Canal S of Ave. 144, along Lakeland Canal S of Ave. 144, along Lakeland Canal S of Kent Ave btwn 12th & 14th S of Lemoore, SW cor Hwy 41 & Jackson S of Lemoore, SE cor Hwy 41 & Jackson S of Lemoore, NE cor Hwy 41 & Jackson S of Lemoore, SE cor Hwy 41 & Jackson S of Lemoore, SE cor Hwy 41 & Jackson S of Lemoore, SE cor Hwy 41 & Jackson S of Lemoore, NE cor Hwy 41 & Jackson S of Lemoore, SE cor Hwy 41 & Ja	Portervile, Hwy 190 x Tule Kriver Terra Bella at Deer Ck. E of Angiola, proposed PNWR Lindsay, SE of, Lewis Creek SE of Tulare, J15, N of Ave 208 El Monte Way x Kings R. Rt. 201 x Kings R. Rt. 201 x Kings R. Dinuba Earlimart, W of, SE end Pixley NWR, S Deer Ck Earlimart, Pixley NWR, Deer Ck Unit N of Pixley NWR, Horse Pasture Unit, 2 sites Earlimart, E of, Church St x Deer Ck. Ave Earlimart, E of, Church St x Deer Ck. Ave Earlimart, B of, Church St x Deer Ck. Ave Earlimart, SE cor Ave 56 & Rd 112 E of Pixley, E of Rd 144 & S of Ave 112 W of Earlimart, SE cor Ave 56 & Rd 112 E of Pixley, E of Rd 144 & S of Ave 112 White River, E of Ducor Kern River Park, NE of Bakersfield, Kern River E of Famoso, Poso Creek, E of old Hwy 65 Hwy 65 x Poso Creek, E of old Hwy 65 Lureline Wells, Poso Creek, E of old Hwy 65 Lureline Wells, Poso Creek
Kings Kings Kings Kings Kings Kings Kings Kings Tulare Tulare	Iulare Tulare Tulare Tulare Tulare Tulare Tulare Tulare Tulare Tulare Tulare Tulare Kern Kern Kern Kern Kern

easiest to find. We checked over 25 floodplain or water edge sites including most historic sites, but no *C. tranquebarica* or other tiger beetles were found. Nearly all of these sites seemed unlikely to support tiger beetle populations because of habitat loss or degradation from agricultural activity, reduced water flow, cattle and human trampling, and/or other land use changes.

We checked over 50 sites with alkali sink or similar saline habitats, including all known historic sites. We focused on the sites near Visalia, Kerman and Helm where many of the earlier collections were made, but most of these and other sites no longer had suitable habitat because of their conversion to agricultural usage, primarily tillage and cattle grazing. We did find several sites in the Kerman area, near the Mendota Wildlife Refuge, with remaining patches of seemingly suitable habitat, but no tiger beetles were found. We and several other collectors also visited the Madera County site between 2003 and 2005 but, because the site was a private ranch, only the peripheral areas were checked and not the interior areas where the beetles were previously found. We found this site to be very densely vegetated with planted grasses, suggesting it may no longer be suitable habitat. Our surveys found *C. t. joaquinensis* at only four sites, three within a 10 sq. km area in Kings County and one in Tulare County. Specific locations of these sites are not given here because of the extreme rarity of this tiger beetle and possible threats from over-collecting.

Kings County sites: The three Kings County sites (designated here as A, B, C), found in late March and April 2005, were scattered fragments of remaining alkali sink habitat near the northeastern edge of the historic Tulare Lake basin, all with similar vegetation and physical characteristics. Vegetation was relatively high (0.5-0.8 m in spring 2005), due to abundant early spring rains, with scattered open bare patches ("mini-playas") of variable size, but usually <100 sq. m) where adults and most larvae were primarily concentrated. The habitat type at site A had common elements of the Valley Grassland, while sites B and C had a greater number of herbaceous perennials. The vegetation included a mix of low, salt tolerant shrubs (Suaeda moquinii, Frankenia salina, Allenrolfea occidentale, and Isocoma acradenia) and Distichlis spicata (saltgrass). Common annual grasses were Bromus spp., Vulpia spp., and Hordeum spp. Common forbs were Atriplex spp., Hemizonia pungens, Lasthenia spp., Lepidium spp., and Spergularia spp. At Kings A we counted a peak number of 35 adults in late March 2005. At Kings B we found only a few adults in March and April 2005 and made a high count of 30-35 in late March 2006. The third site (Kings C) had small numbers of larvae that were probably those of C. tranquebarica, but unfortunately the site was plowed and the habitat found to be destroyed when we checked it in spring 2006.

Tulare County site: A review of aerial photographs of the San Joaquin Valley revealed a potential area for *C. t. joaquinensis* along the eastern edge of the historic Tulare Lake margin. We surveyed the location near Earlimart (Tulare County) in June of 2005 and here we noted apparent *C. tranquebarica* larval burrows associated with the grassland and scattered mini-playas. The vegetation at this site is dominated by Valley Grassland species with very little of the perennial herbaceous cover seen at Kings B. The vegetation included a mix of low, salt tolerant shrubs (*Isocoma acradenia* and *Suaeda moquinii*), *Distichlis spicata* (saltgrass), common annual grasses (*Bromus* spp., *Hordeum* spp., and *Vulpia* spp.), and common forbs (*Atriplex* spp., *Gilia tricolor, Hemizonia* spp., *Lasthenia* spp., *Lepidium* spp., and *Spergularia* spp.). Further surveys in the fall of 2005 confirmed the presence of adult *C. t. joaquinensis*, with a peak count of 22 individuals.

Field notes, behavior, and seasonality: Observations at both Kings and Tulare County sites indicated adults were restricted to the open or edges of the bare alkali patches ("mini-playas") of varying size (20 to 200 sq. m) with usually 1-3 adults per patch. Some patches had standing water or were moist from recent rain, but others had dry surface soil. Most larval burrows (often in small clusters of 2-5) were located at the edges of these bare patches near vegetation. Our field observations and collection records suggest that C. t. joaquinensis has a modified spring-fall seasonal pattern similar to that of the other southern California forms. Adults can be found from late January to mid-February through April, and again in September to November when the new cohort emerges. Most collection records are for March and October (Table 2). The spring activity period is longer than many other spring-fall species but is limited to days when temperatures are near or above 60° F and sunny, and probably when there is some surface moisture. There will thus be frequent extended periods of a week or more during spring when conditions are unfavorable for adult activity. A new adult cohort emerges in late September through October, but the fall emergence may not occur until spring if there is little or no fall rainfall. Our latest observation of adult activity was on November 19, 2005. On that date we dug some adults from apparent larval burrows and observed others going into these burrows. This behavior suggested the adults had emerged earlier and were possibly retreating into these preexisting burrows during periods of unfavorable weather or to spend the cold periods from November to February.

We found large numbers of larval burrows (>150) at both Kings A and B in April 2005, and over 100 at the Tulare site in June 2005. Most were second and third instars and usually present as clusters of 2-8 burrows along the edges of vegetation surrounding the bare patches. A small group of larval burrows were tagged and monitored in 2005. These larvae remained active throughout the summer, but they began plugging their burrows in early September until early October, presumably in preparation for pupation and fall emergence.

Habitat loss, limiting factors, and causes of rarity: Most of the suitable habitat for tiger beetles in the San Joaquin Valley has been lost, primarily due to

the intense agricultural activity and the coincidental disruption of water flow in the rivers and streams. The primary limiting factor for the existing areas of potential alkali sink habitats seemed to be whether or not past land usage had included tillage. None of the sites we surveyed that had experienced significant tillage of the soil had evidence of *C. t. joaquinensis* or any suitable habitat. This was not surprising when considering the immobile nature of larvae and the limited opportunity for reinvasion by adults from the increasingly isolated populations. Some disturbances, however, may only eliminate or reduce habitat quality temporarily. For instance, at one of the sites with beetles, a section had been previously trenched, apparently to alter the drainage pattern.

Tiger beetle habitat in the San Joaquin Valley has also been lost through excessive use of the land for cattle grazing. The main effect of this activity in not the reduction in vegetation but rather the disturbance caused by too many hooves on fragile soil types. Alkaline soils tend to "liquify" during periods of winter and spring rains, and the weight of heavy animals drives their hooves deep into the substrate causing compaction and crushing burrows and/or larvae. Placement of salt licks near alkali playas can also cause animals to congregate near these fragile systems, destroying larval burrows and adult foraging areas. Cattle will also seek out playa areas for water in late spring. These negative perturbations are, however, offset by the benefits of cattle grazing which reduces the vegetation height and density of non-native species to create the open areas needed by *C. t. joaquinensis*.

Another limiting factor for tiger beetles in this area is the loss of open patches due to the growth of annuals plants, some of which are invasive species. The primary invasive species at the current sites are Mediterranean grasses (Bromus diandrus, B. madritensis rubens, B. hordeaceus, and Hordeum murinum leporinum), along with several annual forbs (Bassia hyssopifolia, Erodium spp., Malva parvifolia, and Melilotus indica). In cases where land was not grazed to reduce cover, openings at the margins and between playas were often not present. This choking out of habitat by excessive plant growth was a common problem, and we hypothesize that this is the cause for the extirpation of a C. t. joaquinensis population at the Kaweah Oaks Preserve. Before this site was acquired as a preserve the alkali meadow habitat had several small playa areas kept open by cattle grazing, but one of the early management decisions was to remove grazing cattle in an effort to protect seedling Valley Oaks (Quercus lobata). This allowed the meadow to become overgrown with both native and invasive species. We surveyed this site 5-6 times from 2003-2006 but found no tiger beetles and little or no apparent suitable habitat present. An historic population of Cicindela terricola lunalonga had also been found at this site, but has been extirpated from this and other San Joaquin Valley sites (Kippenhan, pers. comm.). Increased vegetation cover has been previously documented as a significant cause of decline and habitat loss for other tiger beetles, including C. abdominalis (Knisley and Hill, 1994), C. ohlone (Knisley, unpulished studies), and C. debilis (Knisley and Shultz 1997).

Historic notes and current status of C. t. joaquinensis: Since the late Pleistocene, Tulare Lake has been a dominant feature of the southern San Joaquin Valley. Fed by the Kings, Kaweah, Tule, White, and Kern Rivers, it covered approximately 1970 square kilometers and was the largest freshwater lake west of the Great Lakes. It was a shallow body of water (no more than 2 m deep in most areas) and regularly subject to summer evaporation and extreme shoreline fluctuation. At some point during the late Pleistocene or early Holocene, C. tranguebarica probably colonized the saline areas associated with Tulare Lake and nearby foothills. Over time those populations along the lakeshore began to specialize in occupying the summer-dry alkali playas, while those more typical of C. t. vibex continued to occupy alluvial and riparian sites along and into the foothills. These alkali playa tiger beetle populations arose along the eastern margins of Tulare Lake (Guernsey, Earlimart) and the alkali wetlands to the north (Helm, Kerman). With time they became increasingly immaculate and bright green, possibly for camouflage among the tufted spring vegetation (Suaeda moquinii and Lepidium dictyotum) at the playa margins. These populations would have had genetic contact with the green-bronze, well-maculated populations of C. t. vibex along the foothills of the Sierra Nevada and from the Inner Coastal Range (Carrizo Plain, Warthan Canyon). This intergradation of the two subspecies along the riparian corridors that fed Tulare Lake resulted in populations with bright green coloration and more expanded maculations (Coalinga, Dinuba, Bakersfield), and thus considerable variation in maculation pattern in many of the populations.

In today's landscape the immaculate *C. t. joaquinensis* is isolated from surrounding populations by the dramatic changes that have occurred in the past 125 years. The draining of the Tulare Lake and construction of irrigation systems in the 1890s made vast tracts of land available for cultivation. The initial focus of this conversion to agricultural use was land without the high alkalinity associated with the old lakebed. These conversions eliminated most of the saltgrass meadow habitat adjacent to the old riparian corridors. As indicated by collection records, most of the more maculated populations existed in these floodplains associated with prime farmland or along the perimeter of the San Joaquin Valley. As new technologies became available for conversion of the alkaline soils, and greater pressure for new land was exerted, even marginal soils were plowed for agriculture. This has greatly limited the available habitat for the remaining immaculate populations. Little appropriate habitat remains, thus putting the few surviving *C. t. joaquinensis* populations at a high risk for extinction.

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Literature Cited

- Boye, H. P. and R. W. Rust. 1984. Intraspecific and geographic variations in *Cicindela dorsalis* Say (Coleoptera: Cicindelidae). The Coleopterists Bulletin 36: 221-239.
- Boyd, H. P. and Associates. 1982. Checklist of the Cicindelidae. The Tiger Beetles. Plexus Publishers. Marlton, New Jersey. U.S.A. 31 pp.
- Freitag, R. 1999. Catalogue of the tiger beetles of Canada and the United States. NRC Research Press, Ottawa, Canada. 195 pp.
- Kritsky, G. and L. Horner. 1998. Geographic variation in *Cicindela tranquebarica* Herbst (Coleoptera: Cicindelidae). Cicindela 30: 13-32.
- Knisley, C. B. and J. M. Hill. 1992. Effects of habitat change from ecological succession and human impact on tiger beetles. Virginia Journal of Science 43: 335-340.
- Knisley, C. B. and T. D. Schultz. 1997. The biology of tiger beetles and a guide to the species of the South Atlantic States. Special Publication No. 5. Virginia Museum of Natural History, Martinsville, Virginia, U.S.A. 210 pp.
- Pearson, D. L. and F. Cassola. 1992. Worldwide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. Conservation Biology 6: 376-391.
- Pearson, D. L., C. B. Knisley, and C. J. Kazilek. 2006. A field guide to the tiger beetles of the United States and Canada. Identification, Natural History, and Distribution of the Cicindelidae. Oxford University Press. New York, NY, U.S.A. 303 pp.